CARBON DIOXIDE EXCHANGE IN PINUS FLEXILIS AND P. STROBIFORMIS (PINACEAE)

Merry G. Lepper

Department of Botany, University of Wisconsin, Madison 53706

Abstract

Seedlings of *Pinus strobiformis* Engelm. from central Arizona demonstrated significantly higher rates of photosynthesis at 25°C than seedlings of *Pinus flexilis* James from any of five populations from California, Wyoming, or Nevada. The reduction in the rate of carbon fixation in dry soils was significantly less at four temperatures in a Wyoming population of *P. flexilis* than in a *P. strobiformis* population from Arizona. These results are interpreted as responses to the relatively warm and mesic climate of the site where the Arizona seedlings were collected.

Pinus strobiformis (southwestern white pine) and *Pinus flexilis* (limber pine) are closely related white pines of the western United States and Canada (members of the subgenus *Strobus* Lemm. sect. *Strobus* subsect. *Strobi* Loud.: Critchfield and Little, 1966). *Pinus flexilis*, the more northern species, was named in 1823 by James. Engelmann (1848) described *P. strobiformis*, but later (1878) he considered it to be only a variety of *P. flexilis*. Overlapping ranges, morphological similarity, and hybridization have long confused the taxonomy within what has been called the "*Pinus flexilis* complex". Steinhoff (1964) has summarized the nomenclatural and taxonomic history within this group.

The range of *Pinus flexilis* extends from British Columbia to northern New Mexico. *Pinus strobiformis* occurs in New Mexico as well, but its range extends southward into Mexico, as reflected by one of its common names, "Mexican border pine" (Steinhoff, 1964). The distributional patterns of *P. flexilis* and *P. strobiformis* are shown in Fig. 1 [redrawn from Little (1971)], which shows most of the extensive latitudinal ranges of these two species, encompassing more than 17°. One might speculate that differences in latitude as well as other factors would result in distinct *P. flexilis* and *P. strobiformis* habitats. Individuals of these two species might consequently differ in adaptive physiological characteristics. In order to investigate this, gas exchange was studied in seedlings of both species at various temperatures. CO_2 fixation was also investigated in seedlings after the potting soils were allowed to become quite dry.

Methods

Experimental seedlings of *Pinus flexilis* and *Pinus strobiformis* were grown from seeds collected in natural stands in the western

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FIG. 1. Distribution of *Pinus flexilis* and *Pinus strobiformis*, taken from Little (1971). Seedling sources: 1. Mt. Grant; 2. White Mountains; 3. Mt. Pinos; 4. Wind River Indian Reservation; 5, Lincoln Monument; 6. Mogollon Rim.

TABLE 1. HABITAT INFORMATION ON SEED SOURCES FOR EXPERIMENTAL SEED-LINGS. Site numbers refer to text and Fig. 1. Precipitation and temperature data are annual means. D = number of trees of all species per hectare; (f) = *Pinus flexilis*; (s) = *Pinus strobiformis*. Precipitation and temperature data given for Mogollon Rim are from Snowbowl, AZ, 100 km north.

	Site and species	Elev. (m)	Precip. (mm)	Temp. (°C)	Lat. N	Parent rock	D
1	Mt. Grant, NV (f)	3273	175		38°34′	Keratophyre	4
2	White Mtn., CA (f)	3075	325	0.9	37°31′	Granite	150
3	Mt. Pinos, CA (f)	2676			34°45′	Gneiss	140
4	Wind River, WY (f)	2152	200		43°35′	Sandstone	70
5	Lincoln Mon., WY (f)	2618	320		41°14′	Granite	100
6	Mogollon Rim, AZ (s)	2195	557	6.1	34°25′	Limestone	2300

United States (Fig. 1 and Table 1). Species designations of the sampled populations agree with those of Steinhoff (1964), Critchfield and Little (1966), and Little (1971).

Seedlings were grown under uniform conditions in a soil of sand and peat moss. It was necessary to maintain seedlings at relatively cool temperatures and satisfactory conditions for the growth of seedlings were achieved in a growth chamber at 20°C light and 10°C dark with a 15-hour light period. All seedlings were treated during the first year of their growth with one 3-month period of "winter" conditions (7°C and an 8-hour light period). At the time of testing seedlings were about 1.5 years old and were 7.5–15 cm tall.

 CO_2 exchange by seedlings was measured with an infrared gas analyzer using a closed system of air flow, as outlined by Wright (1970, 1974). During all tests the wind speed inside the chamber was 61 meters per minute horizontally at plant height. Light intensity was 75,350 lux. Runs were made at CO_2 levels between 300 and 304 ppm. Each individual plant was tested repeatedly once the chamber attained the proper temperature. Results were not recorded until the plant was acclimated and the rate of CO_2 fixation had stabilized.

Rate of CO_2 fixation in the light was considered to be a measure of net photosynthesis. CO_2 losses due to "dark" respiration as well as to photorespiration are incorporated in this value. Fixation rates have been expressed on the basis of the dry weight of photosynthetic tissue.

Periodic measurements of gas exchange were made in unwatered seedlings as the potting soils progressively dried. The entire pot was weighed each time a plant was tested. Later, when the plant was sacrificed, the potting soil was dried and weighed separately. The oven dried weight was then subtracted from the weight of the soil at the time the plant was tested, and soil moisture percentages could be determined for each test. Tests conducted at a soil moisture of 5.8 percent were chosen for comparative purposes, because at lower levels the *P. strobiformis* seedlings began to die.

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Net photosynthesis and dark respiration were measured at 10, 15, 25, and 35°C in seedlings from each of six populations. Table 1 gives information concerning the sites of origin of experimental seedlings. Gas exchange was measured in four seedlings from each population at each temperature.

Thornthwaite water balance diagrams were used to compare the climates of representative P. flexilis and P. strobiformis sites. Fig. 2A summarizes the yearly precipitation, temperature, and evaporation adjacent to P. flexilis stand 2 in the White Mountains of California. A seven-year temperature and a five-year precipitation record from this weather station (at Crooked Creek Laboratory of the University of California) were averaged in the construction of Fig. 2A (U.S. National Oceanic and Atmospheric Administration, 1972). In comparison, Fig. 2B summarizes this same information for possibly the only long-term weather station with year-round data relevant to P. strobiformis. This is the Snowbowl weather station north of Flagstaff, Arizona, less than 1 km from a P. strobiformis stand. This station is 104 km north of the Mogollon Rim seedling source (site 6). A 12-year record of temperature and precipitation was available from this station for the construction of Fig. 2B (U.S. National Oceanic and Atmospheric Administration, 1972).

RESULTS

Temperature curves for the average net rate of carbon fixation in four seedlings from each of six populations are shown in Fig. 3. The optimum temperature for net photosynthesis in seedlings from each of the *P. flexilis* populations appeared to be near 15° C. Data for 20° C were obtained from only one *Pinus flexilis* population but in this case photosynthetic activity fell off rapidly above 15° C indicating that the optimum temperature is perhaps nearer to 15° C than to 20° C in *P. flexilis*. The optimum temperature for carbon fixation by *P. strobiformis* from site 6, on the other hand, appeared to be nearer 25° C (Fig. 3).

Analysis of variance showed that the difference between one population of *P. strobiformis* and five populations of *P. flexilis* in net rate of photosynthesis was statistically significant (F(1,4) = 8.20, p < 0.05) at a temperature of 25°C.

The Thornthwaite water balance diagram of Fig. 2A shows the development of an average net water deficit of 66 mm during the year in the White Mountains. Snowbowl, Arizona, is a more mesic site, developing an average yearly water *surplus* of 27 mm (Fig. 2B). Although the potential and actual evaporation of the Snowbowl site is high due to relatively high summer temperatures, summer precipitation is also relatively high.

Figure 4 demonstrates the decrease in rate of carbon fixation that



FIG. 2. Thornthwaite yearly water balance diagrams for *Pinus flexilis* and *Pinus strobiformis* sites. A. White Mountains, CA (Crooked Creek Field Station), source of *P. flexilis* seedlings. B. Snowbowl, north of Flagstaff, AZ, a *Pinus strobiformis* site.

occurred in these two taxa after a decrease in soil moisture from a saturated state to a water potential of -20 bars. Four *Pinus strobi-formis* seedlings from Mogollon Rim showed a much greater average depression in photosynthetic rate than did four *Pinus flexilis* seedlings from site 5.

Univariate F tests demonstrated statistical significance in this photosynthetic depression at the 5 percent level at each temperature used. At 10°C, F = 12.7 (p < 0.02); at 15°C, F = 19.6 (p < 0.005); at 25°C, F = 29.4 (p < 0.002); and at 35°C, F = 16.4 (p < 0.01). The Bonferroni approach (Harris, 1975) was used here to correct for the inflation of the probability of making a type-one error when multiple tests are involved.

DISCUSSION

The optimum temperature for carbon fixation is higher in at least one P. strobiformis population than it is in four Pinus flexilis populations, and depression of carbon fixation by low soil moisture was less in one population of P. flexilis at four temperatures. Do these observations support separation of P. flexilis and P. strobiformis? Are they correlated with variations in the habitat?

Steinhoff (1964) concluded that his data on growth rates and morphological characteristics of seedlings, and the characteristics of mature trees and cones, warranted differentiation of P. *flexilis* and P. *strobiformis* at the species level. The data presented here support the existence of two taxa or ecotypes. It may be relevant that Steinhoff found less morphological separation between the two taxa as the



FIGS. 3-4. FIG. 3 (left). Net photosynthesis of *Pinus flexilis* and *P. strobiformis*. Average of four individuals from each of six populations: 1. Mt. Grant; 2. White Mountains; 3. Mt. Pinos; 4. Wind River Indian Reservation; 5. Lincoln Monument; 6. Mogollon Rim. FIG. 4 (right). Depression in rate of net photosynthesis when soil moisture decreased from saturation to -20 bars. Four *P. flexilis* seedlings from Lincoln Monument (site 5) are compared with four *P. strobiformis* seedlings from Mogollon Rim (site 6).

northern boundary of the range of P. *strobiformis* was approached. This he attributed to hybridization and environmental plasticity.

The *P. strobiformis* seedlings that were the subject of the gas exchange studies described here were from near the northern edge of the species range. Opportunities for hybridization of the parent population with *P. flexilis* and latitudinal effects on the habitat may have been maximal, but these northern *P. strobiformis* seedlings were still found to be distinct from *P. flexilis* in adaptive aspects of the process of gas exchange. This occurred in spite of the maintenance of seedlings of both species under uniform environmental conditions.

Evidence such as this supports the coherence of each taxon as a genetic unit despite the possibility of hybridization. The intergradation that Steinhoff (1964) measured in the characteristics of northern P. *strobiformis* and southern P. *flexilis* stands may have been, as he mentions, a plastic response to similar environments, especially as it was most noticeable in mature trees.

Correlations of physiological variations with habitat in these two species are difficult to make. This is due partly to the limited availability of habitat data for *P. strobiformis* and the sampling here of only one population of this species.

Latitude and altitude are determinants of the environment of both species, but their effects may interact. "A decrease in latitude appears

to compensate for increasing altitude of origin for more southern P. flexilis collections" (Steinhoff, 1964, p. 65). So elevation may not be directly correlated with seedling characteristics. In addition, P. flexilis is a pioneer species and seems not to be restricted by elevation as long as competitors are absent (Lepper, 1974). Preston (1947) lists P. flexilis as "socially intolerant", with an elevational range of 1372-3505 m. Britton (1908) describes a range of 1500–3600 meters above sea level. Pinus strobiformis seems also to be variable in its elevational occurrence, although information is difficult to find. Kearney and Peebles (1951) give its elevational range as 1980-3048 m. Pinus strobiformis may, as suggested in Table 1, grow at lower average elevations than P. flexilis (Steinhoff, 1964) but its habitat is probably warmer, if due only to its more southern distribution. Table 1 and Fig. 1 show that P. strobiformis populations are found at lower elevations and latitudes than most P. flexilis populations. Table 1 also shows that the Snowbowl Weather Station, near a P. strobiformis stand, records a higher average annual temperature and precipitation than the *P*. *flexilis* sites for which data were available. The Mogollon Rim, which has no relevant weather station, is at least superficially a very wet area, with frequent summer fog.

Therefore, *Pinus strobiformis* populations may well have a warm and wet habitat relative to *Pinus flexilis* due partly to elevation and latitude. This may explain the higher optimum photosynthetic temperatures and reduced drought tolerance in *P. strobiformis* relative to *P. flexilis*. Other populations of *P. strobiformis* must be sampled, however, before generalizations are made.

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BOOKS RECEIVED AND LITERATURE OF INTEREST

A Flora of California. By WILLIS L. JEPSON. Vol. 4 (2), Rubiaceae. By LAURAMAY T. DEMPSTER. 47 pp., 29 figs., paper. Jepson Herbarium, Berkeley. 1979. \$3.00. A reactivation of the Flora, which was published through Vol. 3, part 2, before Jepson's death in 1946. Vol. 3(3) and Vol. 4(1) have not yet been published. Vol. 4(2) is available with advance payment (checks payable to Regents, University of California) from the Jepson Herbarium, Botany Dept., University of California, Berkeley 94720. An index of the families treated in the Flora to date will be included with each order. Previous volumes (1–3) of the Flora are also available.

ANNOUNCEMENT

Symposium on Air Pollution and Forests

An international symposium on "Effects of Air Pollutants on Mediterranean and Temperate Forest Ecosystems" will be held June 22–28, 1980, in Riverside, CA. The conference will focus on major areas of research in forest air pollution, including the effects of air pollutants on tree growth, on species composition of forest stands, and on forest wildlife, insect pests, and tree diseases. The effects of acid precipitation and heavy metals on forests, and the emission of nitrogen oxides, hydrocarbons, and other natural pollutants from forests will also be discussed. One of the major purposes of the conference is to examine progress in integrating data from diverse, specialized studies into ecosystem-level analyses.

Further information is available from Dr. Paul R. Miller at the Pacific Southwest Forest and Range Experiment Station, 4955 Canyon Crest Drive, Riverside, CA 92507. Pre-registration is advised.